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Incidence of Pre-Emergence Sib-Mating in *Monodontomerus obsoletus, Pteromalus venustus,* and *Tetrastichus megachilidis,* Three Chalcid Parasitoids of the Alfalfa Leafcutting Bee, *Megachile rotundata* (Hymenoptera: Chalcididae)

VINCENT J. TEPEDINO

USDA, ARS, Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah 84322–5310

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Abstract.—Three species of chalcid wasps (*Monodontomerus obsoletus, Pteromalus venustus,* and *Tetrastichus megachilidis*) that parasitize the immature stages of the alfalfa leafcutting bee (*Megachile rotundata*) were studied to determine if females of these spanandrous species are inseminated before they emerge from the host cocoon. In contrast to earlier reports, moderate pre-emergence mating occurred in *M. obsoletus* and *P. venustus* but not in *T. megachilidis*.

INTRODUCTION

Hamilton (1967) constructed what he called "a biofacies of extreme inbreeding and arrhenotoky" for small haplodiploid arthropods in which mating seems normally to take place between siblings. Among the important characteristics Hamilton (1967) listed were: 1) gregarious development of a clutch of siblings; 2) a sex ratio strongly biased towards females (spanandry); 3) protandry; 4) mating immediately after (or occasionally before) females eclose, with males capable of multiple mating and of fertilizing a female's entire egg production with a single insemination; and 5) sperm storage and single mating by females. Hamilton's (1967) explanation for this biofacies hinged upon restricted opportunities for mating in what he termed "viscous" or small, subdivided populations. When the probability of mating between siblings is high, then female parents should produce only as many sons as are necessary to inseminate their daughters.

Three species of hymenopterous protelean parasitoids that attack *Megachile rotundata* (Fabricius) (MR), the alfalfa leafcutting bee, fit Hamilton's (1967) list of attributes quite well; *Monodontomerus obsoletus* Fabricius (Torymidae) (MO), *Pteromalus venustus* Walker (Pteromalidae) (PV), and *Tetrastichus megachilidis* Burks (Eulophidae) (TM). They are haplodiploid and all sting immature MR, usually at the prepupal stage, and then lay numerous eggs either in (TM) or on (MO,

PV) the host. The sex ratios of clutches of parasitoids hatching from individual hosts are spanandrous for MO and TM, but are less so for PV. Mating of at least some females by their protandrous brothers occurs immediately after eclosion as the parasitoids emerge from the host cocoon. Females store sperm and most, if not all, of their egg production can be fertilized by a single insemination. (See Krombein 1967, Hobbs 1968, Hobbs and Krunic 1971, Eves 1970, Whitfield and Richards 1985 for additional details).

Aside from thelytoky, the most extreme development in Hamilton's (1967, 1979) biofacies is for sib-mating to occur within the host cell before the parasitoids emerge. Under such circumstances, opportunities for outbreeding would be all but eliminated. Indeed, if inbreeding is the most favorable option for such species, then pre-emergence mating should be quite common. Hamilton (1967, 1979) cites several examples. The purpose of this study was to determine the incidence of pre-emergence mating in MO, PV and TM.

Methods

Cocoons of MR that had been parasitized by one of the parasitoid species were removed from stock cultures maintained at 29°C on the morning of expected emergence, isolated in clean petri dishes, and placed under constant observation. Several females were removed as soon as they emerged from the host cell, usually in the order of emergence. The remaining adult progeny from each host cell were counted later.

After removal, experimental females were isolated in individual petri dishes and maintained for three days (or prior expiration) at 29°C, and 16L:8D photoperiod with three fresh MR cocoons containing prepupae. Because females will parasitize hosts before being fed, food was not supplied. MR cocoons had previously been radiographed (Stephen and Undurraga 1976) so that those with dead larvae could be detected and removed. After three days, cocoons were placed in individual gelatin capsules and incubated at 29°C, 82% RH until parasites or host emerged. At that time, the number and sex of progeny was recorded.

Results

Monodontomerus obsoletus: Emergence of parasitoids was monitored for 13 parasitized prepupae. In nine (69.2%), males emerged before females. However, the difference in emergence time between the sexes was slight: frequently males and females emerged within seconds of each other; occasionally, males emerged a few minutes earlier. Thus, with respect to emergence from the host cocoon, MO is marginally protandrous.

Seventy-one females were removed and used for the study: 6 females were removed from each of nine cocoons, five were removed from one cocoon, and four were removed from each of three cocoons. These females parasitized 186 of the 213 cocoons provided (87.3%). The 27 unparasitized cocoons contained dead MR larvae when subsequently examined.

Only five of the 71 emergent females (7.0%), from two of the 13 cocoons, had mated prior to the emergence. In one cocoon, only the fifth of six females was mated. She parasitized all three host cocoons offered and produced a total of ten males and 15 females. Female progeny were produced in two of the three cocoons. In the other cocoon, all four females had mated. Together, they parasitized eight of the 12

cocoons offered and produced 12 males and 53 females. It may be relevant to note that the cocoon from which these females emerged had the highest ratio of males to females (1:2) of any of the 13 cocoons used (the next highest ratio was 1:4). However, the only other cocoon which produced a mated female had a male:female ratio of 1:8.

Pteromalus venustus: Protandry appears to be absent in PV: females emerged before males from six of the 13 cocoons monitored. Fifty-eight females were removed for study. PV females displayed much greater variation in the number of hosts parasitized than did MO: 16 females (27.6%) did not parasitize any host cocoons, while ten, 19 and 13 females parasitized one, two, and three cocoons, respectively. Of the 174 cocoons offered, only 87 (50.0%) were parasitized; of the 87 unparasitized cocoons, 44 (50.6%) subsequently produced healthy adult bees. The reasons for this large number of seemingly acceptable, but unattacked, hosts are unclear.

Of the 42 females that did parasitize, 5 (11.9%), from four different cocoons, produced some female progeny. The numbers of adults (males:females) from these four cocoons ranged from 1:8 to 4:4. Together, the five females produced 121 males and 59 females in 13 parasitized cocoons.

Tetrastichus megachilidis: For TM, only four cocoons were monitored. Males emerged from these cocoons before females in three cases. A total of 25 females (10, 5, 5, 5) were removed and isolated with host cocoons. Of these, five parasitized two cocoons, 18 parasitized one cocoon, and two did not parasitize. Thus, of the 75 cocoons supplied, only 28 (37.3%) were used. Of the 47 unused cocoons, 38 (80.9%) subsequently produced live adult bees. TM is the smallest of the parasitoids and the only endoparasite; smaller individuals may have difficulty reaching the host through the cocoon with their ovipositor.

None of the 28 cocoons parasitized produced females.

Discussion

In contrast to previous findings, based on much smaller sample sizes, of no pre-emergence mating in MO or PV (Eves 1970, Hobbs and Krunic 1971), both species displayed a moderate level (7–12%) of within-host cocoon mating. No evidence of pre-emergence mating was found for TM but females from only four cocoons were monitored. For at least two species, however, the behavioral characteristics necessary for complete inbreeding to develop are currently present should such an option become selectively advantageous. Hamilton (1979) has discussed some situations under which higher levels of inbreeding might evolve.

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